

LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF
VALENTIBULLA CALIFORNICA (COQUILLET) (DIPTERA: TEPHRITIDAE)
ON *CHRYSOTHAMNUS NAUSEOSUS* (PALLAS) BRITTON
IN SOUTHERN CALIFORNIA

RICHARD D. GOEDEN, DAVID H. HEADRICK, AND JEFFREY A. TEERINK

Department of Entomology, University of California, Riverside, California 92521.

Abstract.—*Valentibulla californica* (Coquillett) is univoltine and nearly monophagous on *Chrysothamnus nauseosus* (Pallas) Britton (Asteraceae). The larvae develop in short, subsurface mines mostly formed basally in current season's branches, and are not easily detected on infested plants. They cause limited swellings, not readily detectable galls. The egg, second and third instar larva, and puparium are described and figured. The egg, described for the first time for this genus, is unique among nonfrugivorous, California tephritids studied to date because of its ellipsoidal-fusiform shape, acutely tapered posterior, and its prominent, anterior pedicel bearing aeropyles of two distinct diameters. The third instar characteristically is shagreened, i.e. only the integument of the gnathocephalon, the anterior third of the prothorax, and a small area surrounding the posterior spiracular plates are not covered by minute, dome-shaped verrucae. The puparium also maintains the shagreened surface. Premating, mating, and postmating behaviors are described; they are few, and similar to the closely related genus, *Aciurina*. Hymenopterous parasitoids of *V. californica* include three species of chalcidoids reared as primary, solitary, endoparasitoids from isolated puparia: *Eupelmus* sp. (Eupelmidae), *Eurytoma* sp. (Eurytomidae), and *Halticoptera* sp. (Pteromalidae).

Key Words: Insecta, *Valentibulla*, *Chrysothamnus*, biology, taxonomy of immature stages, mating behavior, parasitoids.

This study of *Valentibulla californica* (Coquillett) was undertaken after prolonged searches by RDG for its "galls," as described and pictured by Wangberg (1978), failed repeatedly during the 1980's at various locations in southern California where adults otherwise were swept. Our subsequent findings reported herein address several inconsistencies in the developmental biologies heretofore reported for *V. californica* and its congeners, and add new knowledge on this tephritid otherwise largely known from States outside its type state-locality and namesake.

MATERIALS AND METHODS

Most field studies were conducted with *V. californica* on *Chrysothamnus nauseosus* (Pallas) Britton (Asteraceae) at a Mojave Desert (high-elevation desert) location in the easternmost foothills of the San Bernardino Mountains, 2 km NW of Pioneertown at 1280-m elevation, SW San Bernardino Co., during 1991-93. Samples of branches from plants that from previous dissections had been found to contain larvae and puparia were collected on different dates, months and seasons. Branch samples were trans-

ported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. All larvae and 20 puparia dissected from these branches and eggs obtained from other excised branches used in oviposition studies were preserved in 70% EtOH for scanning electron microscopy (SEM). All other puparia were placed in separate glass rearing vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM later were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH, critically point dried, mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a JEOL JSM C-35 SEM in the Department of Nematology, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cagings were used for longevity studies and oviposition tests in the insectary of the Department of Entomology, University of California, Riverside, at $25 \pm 1^\circ\text{C}$, and 14/10 (L/D) photoperiod. Virgin male and female flies obtained from emergence vials were paired in clear-plastic petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1991) for direct observations, videorecording, and still-photography of their general behavior, courtship, and copulation. Six pairs were held together for at least 14 d and observations were made as opportunity allowed throughout each day. Field observations on adult behavior also were made on *C. nauseosus* at Cajon Junction at 1010-m elevation, San Bernardino Nat. Forest (N section), SW San

Bernardino Co., from 8.iv.1992 to 12.v.1992 for ca. 4 h per day for 2 days per week.

Plant names used in this paper follow Munz (1974); tephritid names follow Foote et al. (1993) except for *Aciurina trixa* Curran (Dodson and George 1986). Nomenclature used to describe the immature stages follows Goeden and Headrick (1990, 1991a, b, 1992), Headrick and Goeden (1990, 1991, 1993), and the telegraphic format of Goeden et al. (1993). Means \pm SE are used throughout this paper. Voucher specimens of reared adults of *V. californica* and its parasitoids reside in the research collections of RDG; preserved specimens of larvae and puparia are stored in separate collections of immature Tephritidae maintained by DHH and JAT.

RESULTS AND DISCUSSION

Taxonomy

Coquillett (1894) first described *V. californica* (as a *Trypeta*). Foote et al. (1993) reviewed the taxonomy and other literature on this species and described and discussed recognition features for the adults. They also provided the key to U.S. and Canadian species used to confirm the identity of our flies. Wangberg (1978) briefly described and provided line drawings of one third-instar larva and one puparium serving to illustrate both *V. californica* and *V. steyskali* Foote and labelled "*Valentibulla* spp.," but without distinguishing these species.

Egg.—Egg body smooth, shiny, white, elongate ellipsoidal-fusiform (Fig. 1A); pedicel peg-like, 0.02 mm long (Fig. 1B); 17 eggs dissected from branches in oviposition cages averaged 0.50 ± 0.006 (range, 0.41–0.52) mm in length, 0.15 ± 0.002 (range, 0.13–0.17) mm in width.

This is the first egg described for any *Valentibulla* species. The egg of *V. californica* differs in shape from previously studied, nonfrugivorous tephritids (Goeden and Headrick 1992; Goeden et al. 1993, 1994a,



Fig. 1. Egg of *V. californica*: (A) habitus, pedicel at left; (B) detail of pedicel, showing aeropyles.

b; Green et al. 1993; Headrick and Goeden 1990) in that it is more acutely tapered posteriorly opposite the pedicel. *Tephritis arizonaensis* Quisenberry has a similar egg body shape, but does not taper as dramatically at the posterior end and the pedicel is not as prominent (Goeden et al. 1993). The egg of *Trupanea californica* Malloch is similar in length and slightly wider, however the shape is elongate-ellipsoidal and the pedicel is smaller (Headrick and Goeden 1991). The egg of *Acurina thoracica* Curran, which is in the same subtribe as *V. californica* (Foote et al. 1993), is shaped very differently and bears distinctly raised polygonal reticulation on its surface (Headrick and Goeden 1993). The pedicel of *V. californica* also differs from all previously examined eggs in that the aeropyle openings are of two dis-

tinct diameters (Fig. 1B). *Tephritis baccharis* (Coquillett) has a similar shaped pedicel twice as long as *V. californica* (Goeden and Headrick 1991b).

Third instar. — Third instar creamy white, shagreened, elongate-ellipsoidal, bluntly rounded apically and posteriorly (Fig. 2A); gnathocephalon conical, smooth with very few rugose pads; pad margins laterad of the mouth lumen partly contiguous and not distinctly raised (Fig. 2B-1); paired dorsal sensory organs dorsomedial of anterior sensory lobes each consisting of a single, dome-shaped papilla (Fig. 2B-2, 2C-1); anterior sensory lobes bear the lateral sensory organ (Fig. 2C-2), terminal sensory organ (Fig. 2C-3), and a papillate sensillum dorsad of the lateral sensory organ (Fig. 2C-4); stomal sense organs lie ventrad of anterior sensory lobes, near the mouth lumen (Fig. 2C-5); lateral (Fig. 2B-3) and ventrolateral sensilla present (Fig. 2B-4), each consisting of a smooth, verruciform sensillum with a central pore; mouth hooks bidentate, teeth stout, conical, rounded apically (Fig. 2B-5, 2D-1); median oral lobe laterally compressed, tapers anteriorly between mouth hooks (Fig. 2B-6), attached basally to labial lobe (Fig. 2D-2); labial lobe bears two pore sensilla (Fig. 2D-3); prothorax smooth anteriorly, covered with minute, dome-shaped verrucae posteriorly; anterior thoracic spiracles located dorsolaterally on posterior margin of prothorax, each consisting of four, obovate papillae (Fig. 2E); meso- and metathorax covered entirely by minute, dome-shaped verrucae; lateral spiracular complex on abdominal segments composed of an open spiracle (Fig. 2F-1), and a single verruciform sensillum (Fig. 2F-2); caudal segment bears posterior spiracular plates (Fig. 2G); plates bear three, oval rimae ca. 0.02 mm long (Fig. 2G-1), and four, short, multibranch interspiracular processes, with three to four branches each, the longest measuring 0.006 mm (Fig. 2G-2); stelex sensilla surround margin of caudal segment in four-dorsal, six-ventral arrangement;

caudal segment additionally bears a pair of compound sensilla ventrad of the spiracular plates consisting of a tuberculate chemosensillum (Fig. 2H-1), and a stelex sensillum (Fig. 2H-2).

Valentibulla californica is only the second species examined by us that is shagreened. *Tomoplagia cressoni* Aczél, which belongs to a different tribe, also is shagreened (Goeden and Headrick 1991a). In *V. californica*, only the integument of the gnathocephalon, the anterior third of the prothorax, and a small area surrounding the posterior spiracular plates are not covered by minute, dome-shaped verrucae. *Aciurina thoracica*, a closely related species (Foote et al. 1993), bears irregular patches of acanthae, but the intersegmental areas are smooth (Headrick and Goeden 1993). *Valentibulla californica* also lacks the rows of minute acanthae that circumscribe the intersegmental areas of several other tephritid species (Goeden and Headrick 1991b, 1992, Goeden et al. 1993, 1994b, Headrick and Goeden 1991).

Foote et al. (1993) placed *Valentibulla* in a new subtribe Eurostina along with *Aciurina* and *Eurosta*. *Valentibulla californica* larvae do resemble *A. thoracica* larvae in many morphological characters (Headrick and Goeden 1993). The gnathocephalon is similar to *A. thoracica*, being smooth with few rugose pads. The median oral lobes are similar, laterally compressed and tapered apically. The gnathocephalon sensilla are very similar in structure and placement; however, there is one noteworthy difference. The anterior sensory lobe in *V. californica* lacks a pit sensory organ. This is the second example of a tephritid with its anterior sensory lobe not bearing the pit sensory organ. *Tomoplagia cressoni*, which is also shagreened, lacks the pit sensory organ (Goeden and Headrick 1991a). Pit sensory organs otherwise are typically similar in size, shape, and placement among tephritid species (Carroll and Wharton 1989, Goeden and Headrick 1990, 1991b, 1992, Goeden et al. 1993, 1994a, b, Headrick and Goeden

1990, 1993). The mouth hooks also differ, being bidentate in *V. californica* and tridentate in *A. thoracica* (Headrick and Goeden 1993). Wangberg (1978) reported *Valentibulla* spp. to have tridentate mouth hooks. The abdominal lateral spiracular complex consists of a spiracle and a single, domed-shaped papillae in *V. californica*, similar to those of *A. thoracica* (Headrick and Goeden 1993), *Trupanea californica* (Headrick and Goeden 1991), *T. nigricornis* (Coquillett), *T. bisetosa* (Coquillett) (Knio and Goeden, unpublished), *N. viridescens* Quisenberry (Goeden and Headrick 1992), *Proceidochares flavipes* Aldrich (Goeden et al. 1994a), and *P. stonei* Blanc and Foote (Green et al. 1993).

Second instar.—Second instar creamy white, shagreened, ovoid in shape, rounded anteriorly and posteriorly (Fig. 3A); gnathocephalon conical, laterally flattened, smooth with a few small rugose pads laterad of the anterior sensory lobes and stomal sense organs (Fig. 3B-1), and a few petals dorsad of the mouth lumen (Fig. 3B-2); paired dorsal sensory organs located dorsomedially to the anterior sensory lobes, consisting of a single dome-shaped papilla (Fig. 3C-1); anterior sensory lobes separated by a medial depression (Fig. 3C), flattened, bearing the terminal sensory organ (Fig. 3C-2), lateral sensory organ (Fig. 3C-3), and a papillate sensillum dorsomedial of the lateral sensory organ (Fig. 3C-4); stomal sense organs lie ventrad of anterior sensory lobes, near the mouth lumen (Fig. 3C-5); mouth hooks bidentate, teeth conical, rounded apically (Fig. 3B-3); median oral lobe laterally flattened, tapered anteriorly between mouth hooks (Fig. 3B-4); prothorax smooth anteriorly, covered with minute, dome-shaped verrucae posteriorly; anterior thoracic spiracles located dorsolaterally on posterior margin of prothorax, each consisting of four obovate papillae (Fig. 3D); lateral spiracular complex not observed; caudal segment bears the spiracular plates, plates bear three oval rimae ca. 0.007 mm long, and four, thorn-

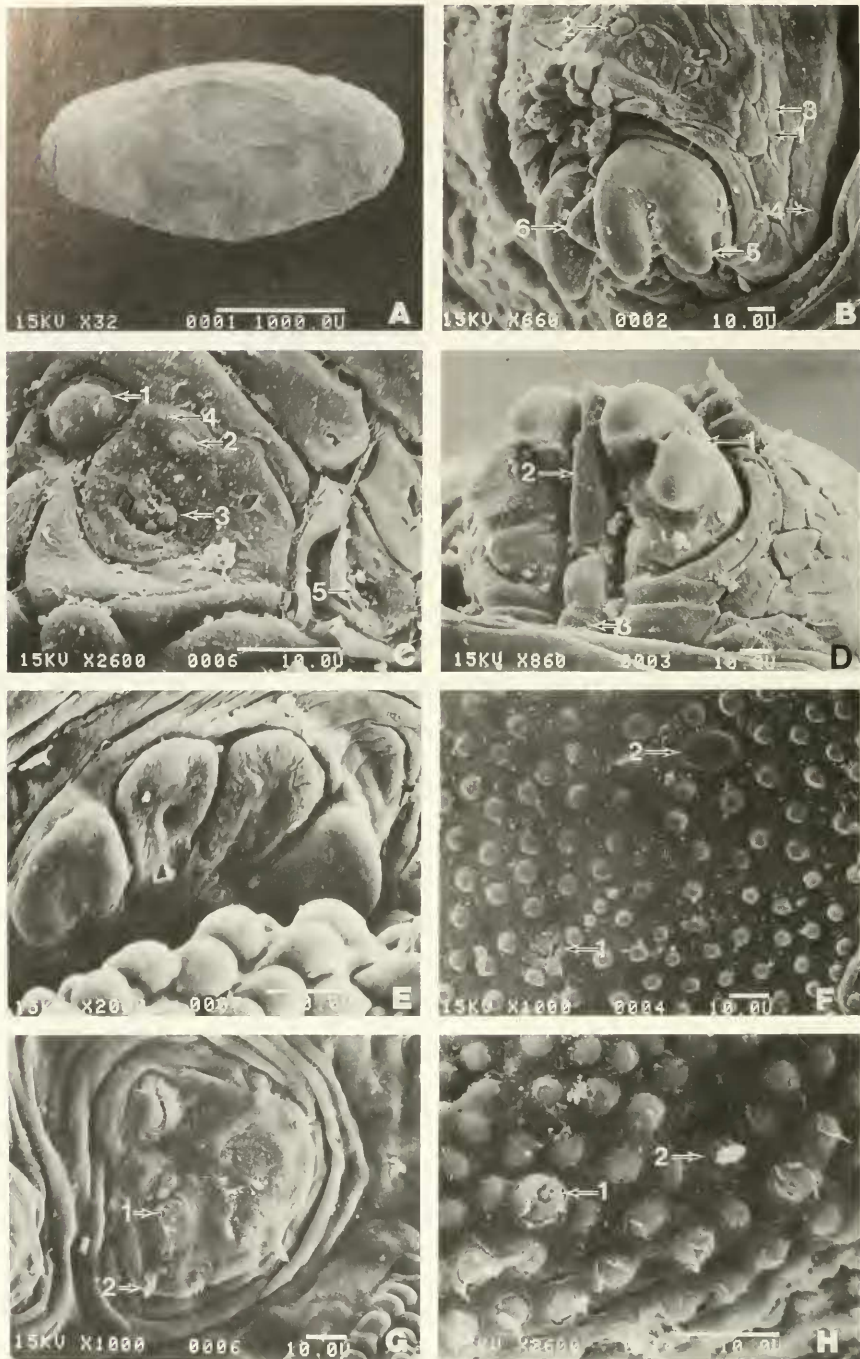


Fig. 2. Third instar larva of *V. californica*: (A) habitus, anterior to left; (B) gnathocephalon, left anterolateral view, 1—rugose pads, 2—dorsal sensory organ, 3—lateral sensillum, 4—ventrolateral sensillum, 5—mouth hooks, 6—median oral lobe; (C) left anterior sensory lobe, 1—dorsal sensory organ, 2—lateral sensory organ, 3—terminal sensory organ, 4—papillate sensillum, 5—stomal sense organ; (D) gnathocephalon, ventral view, 1—mouth hooks, 2—median oral lobe, 3—labial sensilla; (E) anterior thoracic spiracles; (F) lateral spiracular complex,

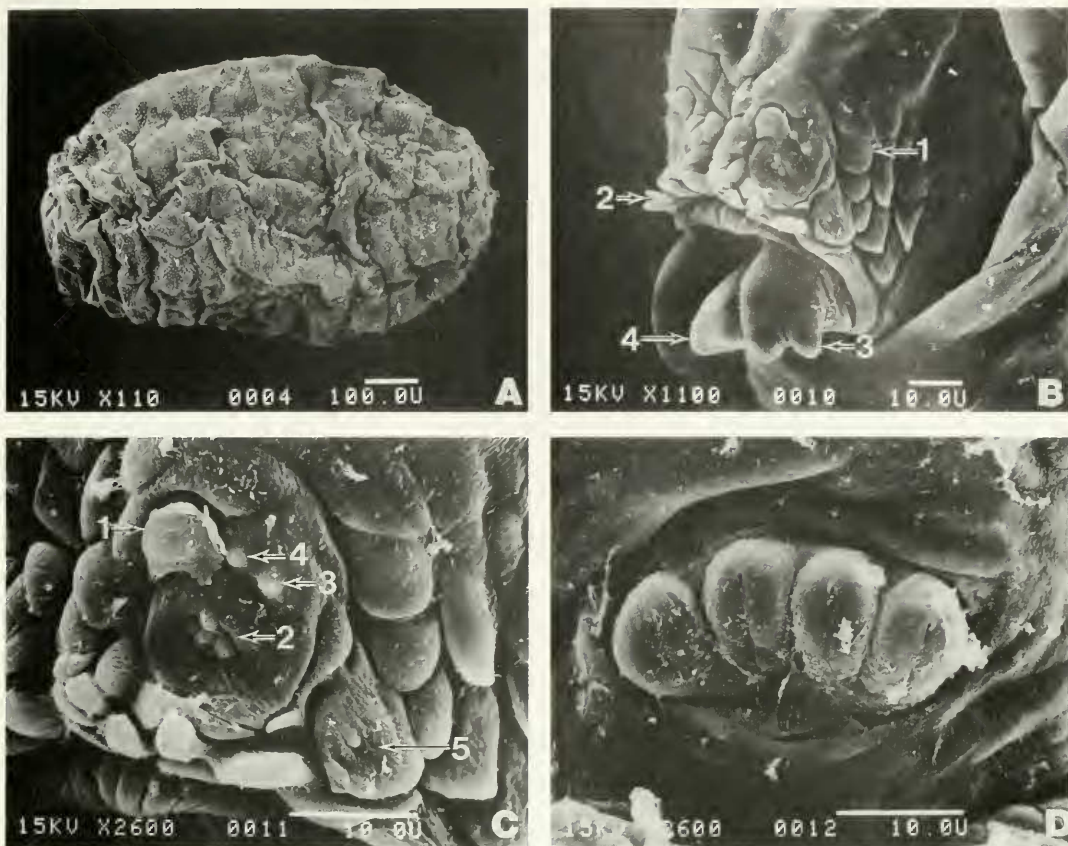


Fig. 3. Second instar larva of *V. californica*: (A) habitus, anterior to left; (B) gnathocephalon, anterolateral view, 1—rugose pads, 2—dorsal petals, 3—mouth hooks, 4—median oral lobe; (C) anterior sensory lobe, 1—dorsal sensory organ, 2—terminal sensory organ, 3—lateral sensory organ, 4—papillate sensillum, 5—stomal sense organ; (D) anterior thoracic spiracles.

like interspiracular processes, longest measuring 0.002 mm; caudal sensilla could not be seen on this specimen.

The features of the second instar of *V. californica* are fairly well-developed morphologically. The gnathocephalon closely resembles that of the third instar. The rugose pads are more widely separated. The petals are present dorsal to the mouth lumen. The mouth hooks are similar in shape to the third instar and bidentate. The me-

dian oral lobe is also similar in shape to that of the third instar. The pit sensory organ was not observed on the anterior sensory lobe of the second instar. The lateral and ventrolateral sensilla were also not observed in the second instar. The lateral spiracular complex could not be seen in the sole specimen examined. The caudal segment, while not pictured, resembled the caudal segment in the third instar.

Puparium.—Puparium creamy white

←
second abdominal segment, 1—spiracle, 2—verruciform sensillum; (G) caudal segment, spiracular plate, 1—rima, 2—interspiracular process; (H) caudal segment, compound sensillum, 1—tuberculate chemosensillum, 2—stelex sensillum.

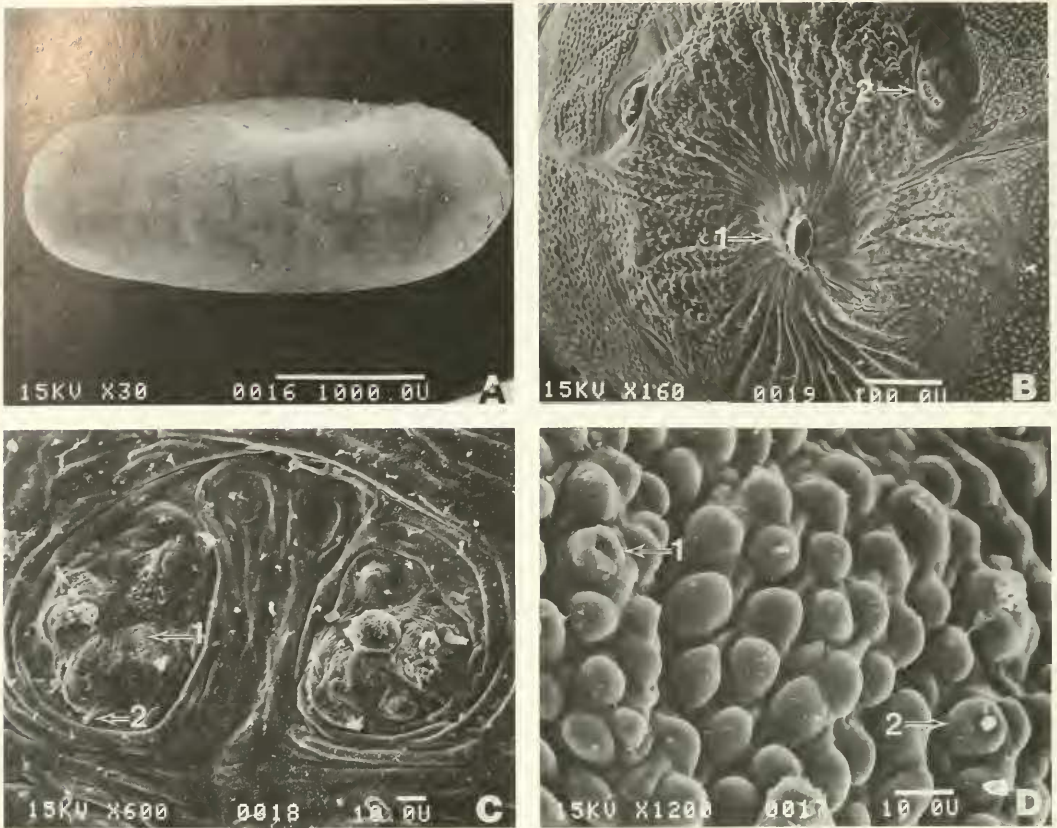


Fig. 4. Puparium of *V. californica*: (A) habitus, anterior to left; (B) anterior end, 1—invagination scar, 2— anterior thoracic spiracles; (C) caudal segment, posterior spiracular plate, 1—rima, 2—interspiracular process; (D) caudal segment, compound sensillum, 1—tuberculate sensillum, 2—stelex sensillum.

when newly formed, darkening to brown, or black with age; elongate-ellipsoidal; minute, dome-shaped verrucae remain distinct (Fig. 4A); 69 puparia averaged 3.14 ± 0.05 (range, 2.3–3.9) mm in length, 1.28 ± 0.02 (range, 0.90–1.59) mm in width; anterior end bears the invagination scar (Fig. 4B-1); anterior thoracic spiracles dorsolaterad of the invagination scar (Fig. 4B-2); posterior spiracular plates bear three oval rimae ca. 0.02 mm in length (Fig. 4C-1), and four, thorn-like interspiracular processes, the longest measuring 0.01 mm (Fig. 4C-2); compound sensilla, i.e. a tuberculate chemosensillum (Fig. 4D-1) and a stelex sensillum (Fig. 4D-2), ventrad of the spiracular plates were retained.

Wangberg (1978) reported that an un-stated number of puparia of *Valentibulla* spp. averaged 3.74 (range, 3.2–4.0) mm in length, considerably longer than our mean and lower limit.

Distribution and hosts

The known distribution of *V. californica* includes the western third of the U.S. as mapped by Foote et al. (1993), who also noted that it had been collected in Baja California Norte. Its known hosts are *Chrysanthamnus nauseosus* (Novak et al. 1967, Wasbauer 1972, Wangberg 1978, Foote et al. 1993) and *C. parryi* (Gray) Greene (Wangberg 1978), a high-altitude species in southern California (Munz 1974) which we

have not examined for the presence of *V. californica*.

Biology

Egg.—The egg is inserted pedicel-last for up to two-thirds its length into a current or preceding year's branch and within or near a prominent axillary bud. The axillary bud was used as a point of purchase on the smooth stems by the ovipositing female in insectary cages, where as many as eight eggs were inserted into one axil. However, based upon dissections of field samples, an average of only 1.4 ± 0.1 (range, 1–4) eggs ($n = 80$) were inserted singly into or near individual buds by one or more females.

Larva.—Upon eclosion, the first instar tunnels apically (17%) or basally (83%) ($n = 72$) into the branch above or below the axillary bud, which subsequently may or may not be killed by larval feeding. The tunnel increases in diameter as the larva grows and deeply scores the woody pith (Fig. 5A), sometimes reaching the opposite epidermis (Fig. 5C), and thus killing the distal part of a thin branch. In most cases, however, the branch above the larva continues its growth apparently unharmed; accordingly, 45 larval tunnels were found upon dissection to begin an average of 10.1 ± 0.9 (range, 1.7–24.5) cm below the apical meristems in live branches. The initial, narrowest part of the larval mine became packed with frass for a distance of 2.3 ± 0.1 (range, 0.8–8.0) mm ($n = 78$) (Fig. 5C). The remainder of the tunnel was open and formed the cell within which the larva fed, presumably on sap conducted to and expressed from the surrounding woody tissues; these excavations are not much larger than the fully grown larvae and puparia (Fig. 5C, D). This type of larval development closely resembles that of *Tephritis arizonaensis* in its branch-tip mines on the woody shrub, *Baccharis sarothroides* Gray (Goeden et al. 1993). It also resembles *Aciurina thoracica*, the larvae of which feed within small branch-tip galls on *B. sarothroides* (Headrick and

Goeden 1993), because of the small excavations formed by both species. However, unlike *A. thoracica* and contrary to Wangberg (1978), we could not bring ourselves to call the feeding sites of *V. californica* "galls." Instead, like Foote et al. (1993), we prefer the description, slight "swelling," or better yet, as Dodson (1987b) described the "gall" of *V. dodsoni* Foote "a rather inconspicuous swelling" of a branch, because this is the only external sign of the larva or puparium within (Fig. 5A, B, C, D, E). Neither do our observations agree with the description for *V. californica* by Wangberg (1978, p. 481) that its "Galls are usually polythalamous and contain 2–6 . . . larvae. Each larva is housed in a cavity that is separated from the others by a tissue wall." Further discussion of this matter follows in the next subsection.

Before pupariation, the fully grown larva of *V. californica* excavates a circular, epidermal window above one end of its cell (Fig. 5G). The larva then pupariates facing the window either basally (36%) or apically (63%, $n = 78$) along the branch.

Pupa.—Eighty-seven full-size cells containing puparia (Fig. 5D, E) measured 4.6 ± 0.1 (range, 2.6–7.1) mm in length and 1.3 ± 0.02 (range, 0.4–1.7) mm in width. Thirty of these cells were found within branches that averaged 2.2 ± 0.2 (range, 0.8–4.4) mm in diameter. The branch diameters just above ($n = 23$) and just below ($n = 30$) these cells differed from the aforementioned stem diameters at the middle of these cells by only 0.4 ± 0.06 (range, 0.0–1.0) mm and 0.3 ± 0.05 (range, 0.0–1.1) mm, respectively. Masked by normal variations in thickness of uninfested branches and stems of *C. nauseosus* at our study site, and by the conspicuous galls caused by other insects, e.g. *Aciurina trixa* Curran (Wangberg 1981, Dodson and George 1986, Dodson 1987b) and several species of Cecidomyiidae (Gagné 1989), the slight swellings symptomatic of *V. californica* are, indeed, "inconspicuous." We further suggest that the gall of *Valenti-*

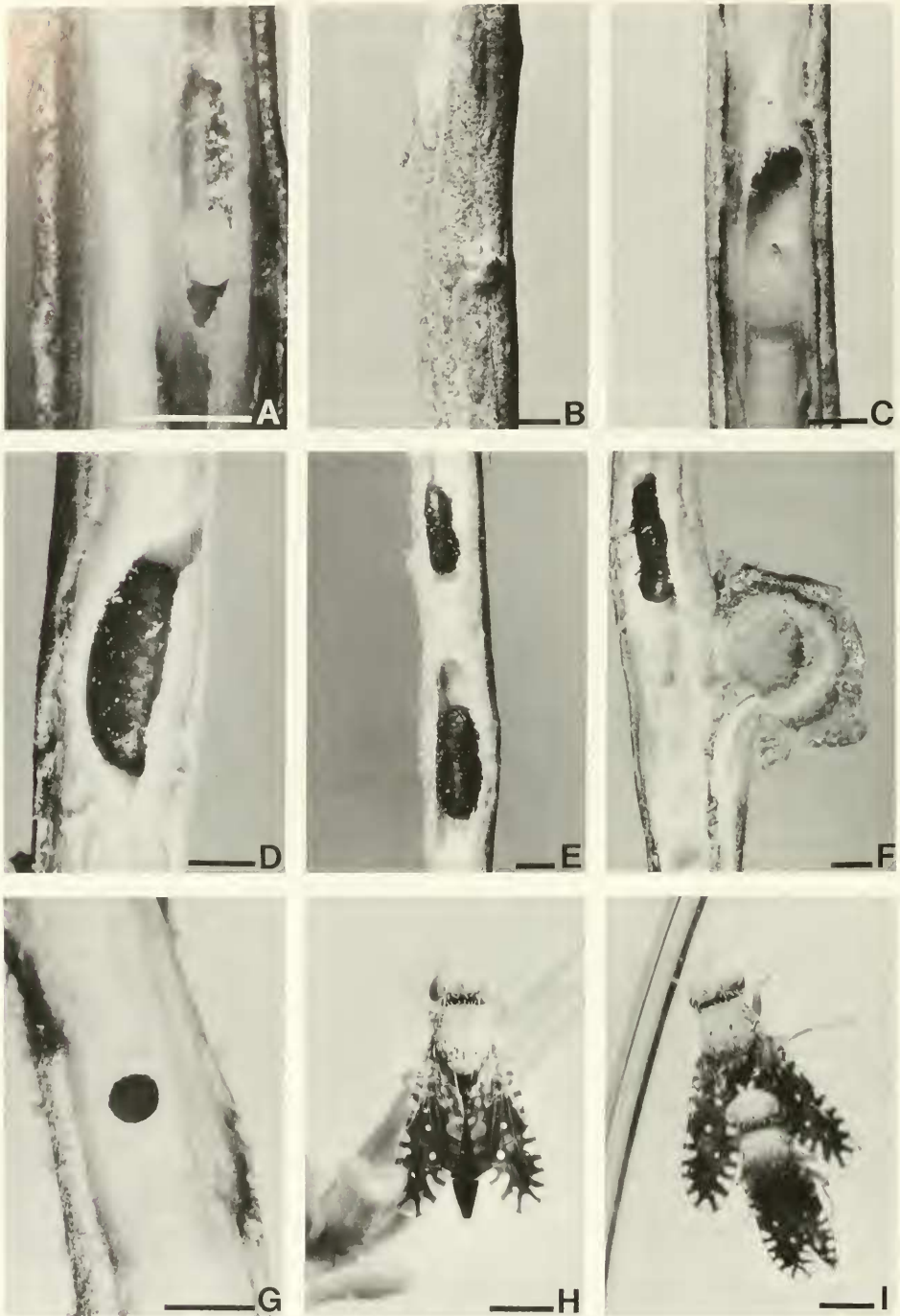


Fig. 5. Life stages of *V. californica*: (A) young larva in branch of *Chrysothamnus nauseosus*; (B) branch where fully grown larva in (C) was found; (D) saggital section of branch with intact puparium in cell facing exit hole still covered by epidermal window; (E) two puparia in cells within same branch; (F) puparium of *V. californica* formed beneath gall of *Aciurina trixa*; (G) exit hole in branch; (H) female adult; (I) mating pair. Line = 1 mm.

bulla spp. pictured by Wangberg (1978) and his description of it quoted above, instead probably refer to a misidentified cecidomyiid gall. This interpretation also may explain differences in the galls described for *V. dodsoni* by Dodson (1987a, b) and for *Valentibulla* spp. by Wangberg (1978). Moreover, *V. californica* larvae and puparia readily were found in juxtaposition to galls of Cecidomyiidae in branches during the present study, and during our laboratory dissections occasionally were located beneath or near galls of *A. trixa* (Fig. 5F, unpublished data). Another ambiguity is the report by Novak et al. (1967) that *V. steyskali* Foote [as *munda* (Coquillett)] larvae form "large, polythalous galls" on stems of *C. nauseosus* in Idaho. These same authors reported *V. californica* from flower heads of *C. nauseosus* in Idaho, where Wangberg (1978) conducted his study. Nevertheless, after 3 years of study, we remain unable to approach individual plants of *C. nauseosus* known from past dissections to harbor *V. californica* at our main study site and with any measure of assurance select branches infested with this tephritid. This alone attests to the inconspicuousness of immature *V. californica* *in situ* in southern California.

Adult.—Egress of the adult (Fig. 5H) entails breaking through the epidermal window covering each exit hole (Fig. 5G). Newly emerged females (Fig. 5H) have immature ovaries ($n = 3$), but within 2 weeks, the numerous, small, irregularly rounded, fat globules found in the haemocoel disappear and are converted into full-size ova. In insectary cages, isolated, unmated, non-ovipositing females (Fig. 5H) lived 45 ± 2.8 (range, 37–56) days; isolated, unmated males lived 49 ± 1.6 (range, 42–55) days.

Wing displays.—Adults of *V. californica* held their wings parted with the posterior wing margins along the abdominal pleura, supinated 45° – 60° relative to the substrate, and with the wing blade bent ventrally at the subcostal break in the costal margin.

Both sexes displayed synchronous and asynchronous supinations with their wing blades in the bent position and with ancillary rotations as described for *Acicurina thoracica* (Headrick and Goeden 1993). Both sexes also displayed abdominal flexures during asynchronous supination, also described for *A. thoracica*, *Paroxynagenalis* (Thomson) (Goeden et al. 1994b), and *Trupanea californica* (Headrick and Goeden 1991).

Mounting, copulatory induction behavior, and copulation.—Males of *V. californica* did not display aggregation behaviors such as abdominal pleural distention, wing displays, territoriality, and male-male combat as described for and commonly observed in other non-frugivorous tephritids (cf. Headrick and Goeden 1990, 1991, 1993, Goeden and Headrick 1991b, 1992b, Goeden et al. 1994b, Headrick et al. 1994). Nor did they initiate courtship displays involving movement of one or more body parts, also commonly observed in non-frugivorous tephritids in either laboratory or field observations (cf. Headrick and Goeden 1990, 1991, 1993, Goeden and Headrick 1991, 1992, Goeden et al. 1993). Males of *V. californica* oriented toward and stalked females from behind, then abruptly jumped onto their dorsa, as described for *V. dodsoni* and *A. trixa* males (Dodson 1987, Headrick and Goeden, unpublished data). As also observed for *A. trixa*, *V. californica* females immediately began rapid walking around the arenas after being mounted, as the males struggled to hold onto them with their front legs. Because mounting by males was so abrupt, they often landed on females in awkward positions that required re-positioning themselves to successfully gain intromission. This readjustment also was observed with *A. thoracica* males (Headrick and Goeden 1993). After mounting and successfully holding onto the female, the male then curled the apex of his abdomen ventrally and placed his epandrium at the apex of her oviscape. His front legs grasped the

widest portion of her abdomen and his middle and hind legs rested on the substrate. The mounted female used her hind legs to push vigorously at the male. The male initiated copulatory induction behavior (CIB) immediately after positioning himself on the female. CIB involved the mounted male drumming vigorously on the venter of the abdomen of the female with his hind legs, unlike *A. thoracica* males who used their middle legs for CIB (Headrick and Goeden 1993). The receptive female exerted her aculeus which pushed the male backward to accommodate its length, because the male kept his abdomen curled ventrally. Insertion of the aedeagus through the ventral flap into the cloacal opening followed aculeus exertion and the female began to slowly retract her aculeus as the male moved forward on the female to assume the copulatory posture (Fig. 5I). During copulation the female intermittently exerted pressure on her aculeus which in turn stimulated the male to begin agitation wing displays. The agitated male lofted his wings, as described for *P. genalis* (Goeden et al. 1994b), 45° above the long axis of his body, while slightly parted and the wing blades were supinated to 90°. Then, the wings were synchronously lowered ca. 10° and raised again without vibration once every half second. The male returned his wings to the typical resting position along his pleura when the agitation stimulus ceased.

After ca. 1 h in copula, the female began to push at the male with her hind legs. This activity signaled the termination of copulation. Disengagement lasted ca. 1 min. The male lifted his abdomen and moved backward on the female; his hind legs were on the substrate and his middle legs were around her ovipositor. He continued to raise his abdomen, disengaged his surstyli from the aculeus, and pulled his aedeagus from the ventral flap while he remained mounted on the female. This disengagement was similar to that described for *P. genalis* males (Goeden et al. 1994b). After disengagement,

the male moved forward on the female and with the aid of his hind legs recoiled the aedeagus. Males initiated CIB behavior in laboratory cagings after ca. 1 min by grasping the ovipositor and drumming it vigorously with the middle legs. Copulations were commonly repeated by the same individuals in less than 1 h; however, no more than two copulations were observed in a single day. After disengagement, females began turning rapidly in circles and resumed buffeting the mounted males with their legs and wings. This latter behavior continued until the male either lost his grip and fell off the female or she again exerted her aculeus. After a second copulation, males fully dismounted from females, which typically displayed aggression by synchronously extending their wings and lunging at males. The only copulation timed from start to finish lasted 1 h.

Field observations.—Adults of *V. californica* were observed on *C. nauseosus* plants along with adults of *Aciurina trixa* and *Proceidochaeres minuta* Snow at the Cajon Junction study site. Adults of *A. trixa* were prevalent at the start of field observations on 8.iv.1992, but diminished in numbers as densities of *P. minuta* increased to 12.v.1992. A total of only eight adults of *V. californica* was observed during all 4 weeks. Males were observed singly on host plants usually in the interior of the crowns and at rest on stems; all three females were observed while ovipositing. No encounters between the sexes were observed. Females oviposited into leaf axils apparently utilizing the same ovipositional niche as *A. trixa* and *P. minuta* females (Headrick and Goeden unpublished data); however, their oviposition behavior was different from these two species. *Valentibulla californica* females did not climb to the tops of branches before ovipositing in the leaf axils as observed for both *A. trixa* and *P. blantoni* (Headrick and Goeden, unpublished data), but rather explored for oviposition sites on the lower portions of branches.

Wangberg (1978) reported that adults of *Valentibulla* spp. on *C. nauseosus* in Idaho were active on host plants throughout the day and displayed their wings toward congeneric individuals. He further described females as vying for the attention of males, which then pursued the females by following behind them. The male then continued to approach the female and if she stood still, he moved behind her and tapped her with his front tarsi. This initial tracking and contact lasted from 1–2 s to 1–2 h. Receptive females remained motionless and males then mounted them. Wangberg (1978) noted that males bent their abdomens ventrally in “an effort to penetrate (the female) with his genitalia.” He also reported that copulations lasted 60–90 min, but did not note any disengagement behavior or repeated copulations by males. Finally, Wangberg (1978) reported that females oviposited under the epidermis of stems rather than into leaf axils as observed in the present study.

Seasonal history.—*Valentibulla californica* is univoltine and nondiapausing on *C. nauseosus* in southern California. Adults emerge in late winter and early spring (February–April) and mating and oviposition commence shortly thereafter; both latter behaviors continue for about 1½ months. The eggs hatch in about a week and the larvae feed and grow slowly through late-spring, summer, and fall (April–November) with pupariation occurring in winter (December–March), as the cycle resumes.

Natural enemies.—Three species of chalcidoid Hymenoptera were reared as primary, solitary endoparasitoids from individual puparia of *V. californica* dissected from *C. nauseosus*: *Eupelmus* sp. (Eupelmidae), *Eurytoma* sp. (Eurytomidae), and *Halticoptera* sp. (Pteromalidae). Wangberg (1978) reported an *Eupelmus* sp. and *Halticoptera* sp. as associates of *Valentibulla* spp. galls, but also *Platygaster* sp. (Hymenoptera: Platygasteridae), known parasitoids of Cecidomyiidae (Clausen 1962) and never reared by us from any Tephritidae in

southern California to date (unpublished data).

ACKNOWLEDGMENTS

We thank A. C. Sanders, Curator of the Herbarium, Department of Botany and Plant Sciences, University of California, Riverside, for identification of plants. Parasitoids were identified by comparison with specimens identified by J. LaSalle, J. Luhman, and C. M. Yoshimoto during their visits or while otherwise associated with the Department of Entomology, University of California, Riverside. We also are grateful to F. L. Blanc and G. Dodson for their helpful comments on earlier drafts of this paper.

LITERATURE CITED

- Carroll, L. E. and R. A. Wharton. 1989. Morphology of the immature stages of *Anastrepha ludens* (Diptera: Tephritidae). *Annals of the Entomological Society of America* 82: 201–214.
- Clausen, C. P. 1962. *Entomophagous Insects*. McGraw-Hill Book Co., Inc., New York and London. Reprint Edition, Hafner Pub. Co., New York.
- Coquillett, D. W. 1894. New North American Trypetidae. *Canadian Entomologist* 26: 71–75.
- Dodson, G. 1987a. Biological observations on *Aciurina trixa* and *Valentibulla dodsoni* (Diptera: Tephritidae) in New Mexico. *Annals of the Entomological Society of America* 80: 494–500.
- . 1987b. Host-plant records and life history notes on New Mexico Tephritidae (Diptera). *Proceedings of the Entomological Society of Washington* 89: 607–615.
- Dodson, G. and S. B. George. 1986. Examination of two morphs of gall-forming *Aciurina* (Diptera: Tephritidae). *Ecological and genetic evidence for species*. *Biological Journal of the Linnean Society* 29: 63–79.
- Foote, R. H., F. L. Blanc, and A. L. Norrbom. 1993. *Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico*. Cornell University Press, Ithaca, New York.
- Gagné, R. J. 1989. *The Plant-Feeding Gall Midges of North America*. Cornell University Press, Ithaca.
- Goeden, R. D. and D. H. Headrick. 1990. Notes on the biology and immature stages of *Stenopa affinis* Quisenberry (Diptera: Tephritidae). *Proceedings of the Entomological Society of Washington* 92: 641–648.
- . 1991a. Notes on the biology, hosts, and im-

- mature stages of *Tomoplagia cressoni* Aczél in southern California. Proceedings of the Entomological Society of Washington 93: 549-558.
- . 1991b. Life history and descriptions of immature stages of *Tephritis baccharis* (Coquillett) on *Baccharis salicifolia* (Ruiz & Pavon) Persoon in southern California (Diptera: Tephritidae). Pan-Pacific Entomologist 67: 86-98.
- . 1992. Life history and descriptions of immature stages of *Neaspilota viridescens* Quisenberry (Diptera: Tephritidae) on native Asteraceae in southern California. Proceedings of the Entomological Society of Washington 94: 59-77.
- Goeden, R. D., D. H. Headrick, and J. A. Teerink. 1993. Life history and descriptions of immature stages of *Tephritis arizonaensis* Quisenberry (Diptera: Tephritidae) on *Baccharis sarothroides* Gray in southern California. Proceedings of the Entomological Society of Washington 95: 210-222.
- . 1994a. Life History and descriptions of immature stages of *Procecidochares flavipes* Aldrich (Diptera: Tephritidae) on *Brickellia* spp. in southern California. Proceedings of the Entomological Society of Washington 96: 288-300.
- . 1994b. Life history and description of immature stages of *Paroxyna genalis* (Thomson) (Diptera: Tephritidae) on native Asteraceae in southern California. Proceedings of the Entomological Society of Washington 96: 612-629.
- Green, J. F., D. H. Headrick, and R. D. Goeden. 1993. Life history and description of immature stages of *Procecidochares stonei* Blanc & Foote on *Viguiera* spp. in southern California. (Diptera: Tephritidae). Pan-Pacific Entomologist 69: 18-32.
- Headrick, D. H. and R. D. Goeden. 1990. Description of the immature stages of *Paracantha gentilis* (Diptera: Tephritidae). Annals of the Entomological Society of America 83: 220-229.
- . 1991. Life history of *Trupanea californica* Malloch (Diptera: Tephritidae) on *Gnaphalium* spp. in southern California. Proceedings of the Entomological Society of Washington 93: 559-570.
- . 1993. Life history and description of immature stages of *Aciurina thoracica* (Diptera: Tephritidae) on *Baccharis sarothroides* in southern California. Annals of the Entomological Society of America 86: 68-79.
- Headrick, D. H., R. D. Goeden, and J. A. Teerink. 1995. Life history and description of immature stages of *Euaesta stigmatica* (Diptera: Tephritidae) on native ragweeds (*Ambrosia* spp.) in southern California. Annals of the Entomological Society of America 88: 55-71.
- Munz, P. A. 1974. A Flora of Southern California. University of California Press, Berkeley.
- Novak, J. A., W. B. Stoltzfus, E. J. Allen, and B. A. Foote. 1967. New host records for North American fruit flies (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 69: 146-148.
- Wangberg, J. K. 1978. Biology of gall-formers of the genus *Valentibulla* (Diptera: Tephritidae) on rabbitbrush in Idaho. Journal of the Kansas Entomological Society 51: 472-483.
- . 1981. Gall-forming habits of *Aciurina* species (Diptera: Tephritidae) on rabbitbrush (Compositae: *Chrysothamnus* spp.) in Idaho. Journal of the Kansas Entomological Society 54: 711-732.
- Wasbauer, M. W. 1972. An annotated host catalog of the fruit flies of America north of Mexico (Diptera: Tephritidae). California Department of Agriculture, Bureau of Entomology, Occasional Papers 19: 1-72.